The effects of adding fat to diets of lactating dairy cows on total-tract neutral detergent fiber digestibility: A meta-analysis

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ABSTRACT

The objective of this meta-analysis was to determine the effects of supplemental fat on fiber digestibility in lactating dairy cattle. Published papers that evaluated the effects of adding fat to the diets of lactating dairy cattle on total-tract neutral detergent fiber digestibility (ttNDFd) and dry matter intake (DMI) were compiled. The final data set included 108 fat-supplemented treatment means, not including low-fat controls, from 38 publications. The fat-supplemented treatment means exhibited a wide range of ttNDFd ($49.4\% \pm 9.3$, mean $\pm$ standard deviation) and DMI ($21.3 \text{ kg/d} \pm 3.5$). Observations were summarized as the difference between the treatment means for fat-supplemented diets minus their respective low-fat control means. Additionally, those differences were divided by the difference in diet fatty acid (FA) concentration between the treatment and control diets. Treatment means were categorized by the type of fat supplement. Supplementing 3% FA in the diet as medium-chain fats (containing predominately 12- and 14-carbon saturated FA) or unsaturated vegetable oil decreased ttNDFd by 8.0 and 1.2 percentage units, respectively. Adding 3% calcium salts of long-chain FA or saturated fats increased ttNDFd by 3.2 and 1.3 percentage units, respectively. No other fat supplement type affected ttNDFd. Except for saturated fats and animal-vegetable fats, supplementing dietary fat decreased DMI. When the values for changes in ttNDFd are regressed on changes in DMI there was a positive relationship, though the coefficient of determination is only 0.20. When changes in ttNDFd were regressed on changes in DMI, within individual fat supplement types, there was no relationship within calcium salt supplements. There was a positive relationship between changes in ttNDFd and changes in DMI for saturated fats. Neither relationship suggested that the increased ttNDFd with calcium salts or saturated FA was due to decreased DMI for these fat sources. A

subset of the means included measured ruminal neutral detergent fiber digestion. Analysis of this smaller data set did not suggest that ruminal neutral detergent fiber digestibility is depressed by fat supplementation more than ttNDFd. Adding fats, other than those with medium-chain FA, consistently increased digestible energy density of the diet. However, due to reduced DMI, this increased energy density may not result in increased digestible nutrient intake.

Key words: NDF digestibility, dietary fat, DMI, dairy cow

INTRODUCTION

The NRC (2001) and literature reviews (Palmquist and Jenkins, 1980; Jenkins, 1993) cite dietary fat as having a negative effect on fiber digestibility in lactating dairy cattle. This conclusion is primarily based on evidence showing that fat decreases NDF digestibility in steers and sheep (Ward et al., 1957; Devendra and Lewis, 1974; Jenkins and Palmquist, 1984). Overall, evidence is lacking that the same decrease in fiber digestibility occurs in lactating dairy cattle when fat is supplemented (Palmquist, 1991; Brask et al., 2013). Some studies have found that fat significantly decreased total-tract NDF digestibility (ttNDFd) in lactating dairy cattle, but the magnitude of the decrease was minimal (Ueda et al., 2003; Martin et al., 2008; Reve-neau et al., 2012). A published summary of the effect of fat addition on fiber digestion in lactating dairy cows is not available.

The NRC (2001) cites unsaturated fats as having a more negative effect on rumen fermentation compared with calcium salts and hydrogenated fats. This is attributed to possible differences in the effects on microbial populations as it is known that UFA can affect microbial growth rates in vitro (Maia et al., 2007). Additionally, increasing the particle size of the fats or oilseeds is recognized as a possible mechanism for decreasing negative effects of UFA (Weld and Armentano, 2016). The presence of additional dietary calcium or fat in the form of calcium salts, rather than fatty acids (FA), has been shown to reverse negative effects of fat

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on fiber digestibility (Ward et al., 1957; White et al., 1958; Jenkins and Palmquist, 1984).

The objective of this meta-analysis is to provide a quantitative summary of the effects of fat supplementation on ttNDFd in lactating dairy cattle reported in the literature. Despite the presence of reviews on the effects of fat on ruminal fermentation, they do not offer a quantitative summary or analysis of the effects of fat on fiber digestibility. As the complexity of nutrient requirement models intensifies, a quantitative understanding of the effects of fat supplementation to the diets of high-producing dairy cattle will be necessary.

MATERIALS AND METHODS

Study Selection

Papers published in English between 1980 and 2015 that reported ttNDFd in lactating dairy cattle fed fat-supplemented diets and a corresponding lower-fat control diet were compiled using Google Scholar, Web of Knowledge, and the *Journal of Dairy Science* as search engines. Combinations of the following search terms were used: fat, fatty acid, fiber digest, dairy, cow, oil, tallow, Ca salts, hydrogenated, saturated, canola, flaxseed, linseed, sunflower, soybean, and rapeseed. Relevant citations from these papers were included as well.

Treatments included in the final analysis reported ttNDFd and dietary FA or ether extract (**EE**); had a

corresponding low-fat control diet with a similar forage-to-concentrate ratio as the treatment diet(s) (within 5 percentage points); used lactating dairy cows; and supplemented fat orally. We excluded studies supplementing fat in the form of full-fat oilseeds of any particle size due to the possible confounding effect of altering the source of NDF in the diet and oil availability.

We formed supplemental fat categories based on the descriptions and FA compositions of fat supplements reported in the studies, which resulted in some variation of FA composition within categories (Table 1). Calcium salts of palm oil were categorized separate from calcium salts of long-chain FA (**LCFA**) because of the differing FA profile. Oils and calcium salts of LCFA include all seed oils, but not palm oil. Oleamide treatments were included in the analysis for the purpose of study effects, but the results are not reported because there were only 2 treatments. One publication did not report the standard error (**SE**) of ttNDFd, so SE was calculated using the mean square error reported (Smith et al., 1993).

Statistics

Many studies fed more than 1 fat type at similar dietary concentrations with a shared lower-fat control diet, whereas relatively few studies examined multiple levels of the same fat type (Figure 1). For all studies, each fat treatment mean and its corresponding control mean within a study were summarized into 1 observa-

Table 1. Description of the fat treatment means included in the data set

Variable	Mean	SD	Minimum	Maximum	n ²
ttNDFd ¹ (%)	49.4	9.3	28.8	66.8	98
DMI (kg/d)	21.3	3.5	13.4	27.8	93
Acetate:propionate ratio	2.73	0.45	1.46	3.61	63
Diet characteristics (% of DM)					
Fatty acids	6.2	1.3	3.8	10.0	98
Δ FA ³	3.3	1.3	1.1	6.6	98
NDF	32.4	4.3	22.5	43.3	98
CP	17.1	1.3	14.1	20.8	98
NFC	36.2	4.9	22.6	48.9	98
Calcium	1.0	0.2	0.5	1.3	47
Forage level	49.6	7.7	35.0	67.0	98
Production parameters					
Milk (kg/d)	32.3	7.5	14.1	57.7	89
Fat (%)	3.36	0.47	2.37	4.67	89
Protein (%)	3.07	0.19	2.71	3.54	87
DIM	101	52	31	213	82
Total-tract apparent digestibility (%)					
Fatty acids	67.3	11.3	36.7	92.7	56
Ether extract	77.6	9.8	59.6	93.0	32
OM	67.4	4.7	54.1	77.1	75

¹ttNDFd = total-tract NDF digestibility.

²n = number of fat treatments.

³ Δ FA = change in dietary fatty acid concentration from the lower fat control.

Figure 1. Total-tract NDF digestibility (ttNDFd) versus dietary fatty acid (FA) content (% DM). (A) Saturated fat; (B) calcium salts of palm oil (solid line), medium-chain FA (dotted line); (C) calcium salts of long-chain FA, oils (solid lines), oleamides (dashed lines); (D) oil; (E) tallow; (F) animal-vegetable fat (dotted line), C16 (solid line). Lines connect data points of treatment within a study. Fat types within a study generally share the same low-fat control. Numbers correspond to a low-fat control (Table 2) and are numbered in order from the greatest ttNDFd to the least ttNDFd.

tion, calculated as the ttNDFd treatment mean minus the ttNDFd mean of the control diet (Δ ttNDFd), with a similar calculated mean difference for DMI (Δ DMI).

For studies that reported EE rather than FA content of the diet, 1 percentage unit was subtracted from the EE to estimate FA (NRC, 2001). This should have

minimal effect on the difference in FA content between control and treatment diets (added FA, ΔFA), but could have had a larger effect on FA concentration if absolute concentrations were used across studies in a linear regression approach. Studies were weighted by the inverse of the SE of ttNDFd for both ttNDFd and DMI analysis.

The ΔDMI and ΔttNDFd were divided by ΔFA to give a change in ttNDFd ($\Delta\text{ttNDFd}/1\%\text{FA}$) or DMI ($\Delta\text{DMI}/1\%\text{FA}$) per 1-percentage-unit increase in dietary FA. The assumption of a linear effect of fat on ttNDFd and DMI was made; this was validated by examining the effect of ΔFA on ΔttNDFd and ΔDMI .

Analysis was conducted using SAS 9.4 (SAS Institute Inc., Cary, NC). Significant effects for each model were determined using the MIXED procedure by manual stepwise deletion. Independent variables eligible for inclusion were (expressed as percent of diet DM unless otherwise noted) forage level, corn silage level, NDF, CP, NFC, FA, ΔFA , and proportion of corn silage (percent of forage level). All independent variables were corrected by subtracting the mean value of all studies so that they were distributed around zero, as the intercept of the model was forced through zero.

The first model was a regression of ΔttNDFd on ΔFA . Fat supplementation must have been of only 1 type (for example oil or C16, but not both). The intercepts for all fat types were forced through zero, which represents no fat addition or control. The model was

$$Y_{ij} = B_i X_i + C_j Z_j + s_j + e_{ij},$$

where Y_{ij} is the ΔttNDFd of the j th study within the i th fat type; $B_i X_i$ is the slope of the i th fat supplement due to ΔFA ; $C_j Z_j$ is the effect of dietary parameter; s_j is the random effect of the j th study; and e_{ij} is the residual error. The slope of each fat type (B_i) was tested to determine if it was different from zero. No dietary parameters besides CP were significant in the final model. The quadratic effect of ΔFA was tested and not found to be significant.

The second model determined the least squares means for $\Delta\text{ttNDFd}/1\%\text{FA}$. Fat supplementation again must have been only of 1 type. The MIXED procedure was used with the model

$$Y_{ij} = \mu + B_i + s_j + e_{ij},$$

where Y_{ij} is the $\Delta\text{ttNDFd}/1\%\text{FA}$ of the j th study within the i th fat type; μ is the overall mean; B_i is the effect of the i th fat type; s_j is the random effect of study and e_{ij} is the residual error. Least squares means were

determined and the Bonferroni adjustment was used to determine which means were significantly different.

The same models were used for DMI, weighted by the SE of ttNDFd, with the exception that the first model did not include the effects of dietary CP on ΔDMI .

The REG procedure was used to determine if there was a significant relationship between ΔttNDFd and ΔDMI . Treatments with multiple sources contributing to fat supplementation were included in addition to those with a single source. Least squares means and slopes were tested to determine if they were significantly different from zero (null hypothesis: fat addition has no effect). Significance was declared for $P \leq 0.05$ and a tendency was declared for $0.05 < P \leq 0.10$.

TDN Calculations

Predicted changes in TDN concentration and intake due to supplementation of each fat type were modeled using the least squares means of $\Delta\text{DMI}/1\%\text{FA}$ and $\Delta\text{ttNDFd}/1\%\text{FA}$. A low-fat control diet was designed that contained 43% NFC, 30% NDF, 17% CP, 2% FA, and 8% ash on a DM basis. The total-tract digestibility of nutrients were assigned to be 75% for FA (Boerman et al., 2015), 65% for CP (Lapierre et al., 2005), and 80% for NFC (calculated based on other digestibilities), and were not changed with fat supplementation. The control diet was assigned the mean ttNDFd and DMI (49.6% and 22.4 kg/d, respectively) from the controls of the studies compiled. The fat-supplemented diets were simulated by substituting 3% FA for 3% NFC. The digestibility of fat from different sources was not an objective of this review, and fat digestibility of 75% was not changed depending on the type of fat supplemented; therefore, these estimated changes in TDN will undervalue more digestible fat sources and over value poorly digested fat sources. Dry matter intake and ttNDFd were the only values changed for different fat supplement types.

RESULTS AND DISCUSSION

Data

The compiled studies represent a large range of production parameters and digestibilities (Tables 1 and 2, Figure 1). Some of the numerical differences may be attributed to the large range of average DIM and the range of time over which studies were published (1987–2015). Some of the numerical differences in ttNDFd among studies are likely due to variations in methodology, which have been shown to affect estimates of digestibility (Harvatiné and Allen, 2006; Lee

Table 2. Citations of studies included in the data set with the corresponding ranking of the total-tract NDF digestibility (ttNDFd) of the control (Figure 1) and a description of the treatments

Citation	Rank ¹	Fat types (L) ²
Enjalbert et al. (1997)	1	CSLCFA (1), CSP (1)
Benchaa et al. (2015)	2, 17	Oil (2)
Doreau et al. (1993) ³	3	CSLCFA (1), Oil (1)
Avila et al. (2000) ³	4	AV (1), Tal (1)
Smith et al. (1993)	5, 9, 14, 16, 29, 30	Tal (6)
Brask et al. (2013) ³	6	Oil (1)
Ueda et al. (2003) ³	7, 22	Oil (2)
Aldrich et al. (1997)	8	CSP (1)
Reveneau et al. (2012) ³	10, 15	AV (2), MCFA (2)
Kargar et al. (2012)	11	AV (1), C16 (1)
Palmquist (1991)	12	AV (1), CSP (1), Tal (1), Sat (2)
Chouinard et al. (1998)	13	CSLCFA (3)
Pantoja et al. (1994) ³	18	AV (1), Sat (1)
Weiss and Wyatt (2004)	19	CSP (2), C16 (2)
Weiss et al. (2011)	20	CSP (1), C16 (1), Sat (1)
Drackley and Elliott (1993)	21	Sat (3)
Do Prado et al. (2015)	23, 34	Oil (2)
Chelikani et al. (2004) ³	24	Oil (1)
Freitas et al. (2014)	25	Oil (1), CSP (1)
Elliott et al. (1996)	26	C16 (2), Sat (1), CSP (1)
Pantoja et al. (1996)	27	Tal (1), Sat (1)
DePeters et al. (1987)	28	Tal (2)
Ruppert et al. (2003)	31, 46	Tal (4)
Martin et al. (2008)	32	Oil (1)
Weigel et al. (1997)	33	Tal (4)
Drackley et al. (1994)	35	Tal (3)
Hollmann and Beede (2012)	36	AV (1)
Schauff et al. (1992)	37	Tal (2)
Elliott et al. (1994)	38	Tal (2)
Faciola and Broderick (2013)	39	MCFA (3)
Benchaa et al. (2012)	40	Oil (3)
Piantoni et al. (2015)	41	Sat (1)
Harvatine and Allen (2006) ³	42, 43	CSLCFA (2), Sat (2)
Jenkins (1998)	44	Oil (1), Oleamide (1)
Deluca and Jenkins (2000)	45	Oil (1), Oleamide (1)
Rico et al. (2014)	47, 50	CSP (2), C16 (2)
Eastridge and Firkins (2000)	48	Tal (1), Sat (3)
Piantoni et al. (2013)	49	C16 (1)

¹Multiple rank numbers indicate multiple control treatments differing in forage level, forage type or protein level.

²AV = animal-vegetable fat; Sat = saturated fat; CSP = calcium salts of palm; CSLCFA = calcium salts of long-chain fatty acid; MCFA = medium-chain fatty acid (C12 and C14); Tal = tallow; L is the number of dietary levels of that particular fat supplement.

³Indicates that the publication reported rumen NDF digestibility.

and Hristov, 2014). This should not have significantly affected our data due to the inclusion of random study effects and the analysis of differences between the control and treatment.

There were numerical differences in the mean of the dietary FA concentrations of the controls and the differences between the controls and treatments across studies and fat types (Table 3), but these were accounted for by the analysis of the data as slopes. There were also numerical differences in the means of the controls of ttNDFd and DMI among fat types (Table 4), but these differences were assumed to have little impact on the effect of fat supplementation on ttNDFd or DMI.

Most of the fat categories were fairly uniform in FA profile. However, the C16 category contained fat supple-

ments with proportions of C16 ranging from 49 to 99% (67.8 ± 17.8 , mean $\pm$ SD) of total FA, and the oils and calcium salts of LCFA contained a variety of 18-carbon FA unsaturation levels. There are only 3 fat categories that had both FA and triglycerides (**TG**) within them: saturated fats, medium-chain FA (**MCFA**; 12- and 14-carbon FA), and C16. None had many FA treatments compared with the number of TG treatments. Therefore, we drew no conclusions about the differing effects of dietary TG versus FA based on the data, but it is an area that should be investigated further. This may be an important distinction, as calcium salts are a nonesterified FA, but are often compared with TG of similar FA profile rather than to FA. Jenkins and Palmquist (1984) showed that FA have more negative

Table 3. Raw means of dietary fatty acid (FA) concentration of treatment and control diets and the primary and secondary (1° and 2°) FA present in each supplement

Fat supplement type	N ¹		Diet FA (% DM, mean ± SD)			Δ FANFC ² (% DM)	FA profile	
	Trt	Pub	Control	Treatment	Δ FA		1°FA	2°FA
MCFA ³	5	2	3.0 ± 0.1	6.9 ± 1.3	3.9 ± 1.3	2.0 ± 2.0	12:0	14:0
Oil	16	11	2.1 ± 0.5	5.8 ± 1.2	3.7 ± 1.4	2.4 ± 3.0	18:3	18:1
C16	9	4	3.2 ± 0.4	5.9 ± 1.0	2.7 ± 1.1	1.4 ± 1.5	16:0	18:1
Animal-vegetable	7	6	3.0 ± 0.8	7.0 ± 1.8	4.0 ± 1.6	0.7 ± 0.9	18:1	18:2
Tallow	27	11	3.1 ± 1.0	6.0 ± 1.2	3.1 ± 1.2	0.9 ± 2.1	18:1	16:0
Calcium salts palm	9	7	3.2 ± 0.7	6.5 ± 1.4	3.3 ± 1.4	0.7 ± 0.7	16:0	18:1
Calcium salts LCFA ⁴	8	4	3.0 ± 1.6	5.9 ± 1.9	2.9 ± 1.5	0.3 ± 1.5	18:2	18:1
Saturated fat	15	8	3.1 ± 1.0	6.8 ± 1.3	3.7 ± 1.2	0.4 ± 2.5	18:0	16:0
Overall mean ⁵	98	38	2.9 ± 1.0	6.2 ± 1.3	3.3 ± 1.3	0.8 ± 1.7	—	—

¹Trt = treatment means; Pub = publications.

² Δ FANFC = change in the sum of NFC and FA fractions (treatment – control).

³MCFA = medium-chain FA, C12 and C14.

⁴LCFA = long-chain FA.

⁵Includes the oleamide treatments (n = 2).

effects on total-tract ADF digestibility compared with calcium salts of the same FA profile. These data should be applied to current ttNDFd cautiously due to differences between ADF and NDF digestibility, as well as the low production (18.3 kg/d), in the 1984 study.

Prior to classification of fat supplementation and summary of the treatment means as differences from the controls, an attempt was made to do the analysis as described by St. Pierre (2001) using the dietary FA (% DM) of the control and treatment diets. However, due to the differing effects of types of fat and the limited range over which FA are supplemented, no additional useful information was gained from consolidating the effects of fat into one linear model. Additionally, the attempt was made to analyze the data using the relative concentrations of specific FA in the supplements or diets. However, the number of studies reporting the necessary information was minimal. Therefore, the decision was

made to determine the effects for specific categories of fat supplements. The addition of published literature containing FA profiles of the diet would be beneficial in further evaluating the effects of specific FA on NDF digestibility.

Total-Tract NDF Digestibility

Change in FA within type of fat was significant as a linear effect in the model for Δ ttNDFd ($P < 0.05$). Total FA content of the treatment diet did not provide a better model fit than Δ FA, and Δ FA as a quadratic effect was not significant ($P > 0.10$). Medium-chain FA and oil both significantly decreased ttNDFd, though the magnitude of the decrease in ttNDFd was much less for oil (0.6 percentage units/1% FA) than that for MCFA (2.7 percentage units/1% FA; Table 5, Figure 2). Saturated fats tended to increase ttNDFd (0.4 per-

Table 4. Unweighted means of total-tract NDF digestibility (ttNDFd) and DMI by fat supplement type

Fat supplement type	ttNDFd (% , mean ± SD)				DMI (kg/d, mean ± SD)			
	N	Control ¹	Treatment	Δ	N	Control ¹	Treatment	Δ
MCFA ²	5	49.5 ± 6.9	38.5 ± 7.7	−11.0	5	22.5 ± 2.6	18.5 ± 3.4	−4.0
Oil	16	50.5 ± 8.8	48.2 ± 10.3	−2.3	16	19.4 ± 2.9	18.4 ± 2.7	−1.0
C16	9	46.5 ± 9.5	45.5 ± 7.9	−1.0	9	24.5 ± 2.6	24.1 ± 2.3	−0.4
Animal-vegetable	7	56.1 ± 5.3	56.1 ± 7.0	0.0	6	22.8 ± 3.5	22.0 ± 3.5	−0.8
Tallow	27	48.6 ± 6.7	49.0 ± 7.8	+0.4	26	23.1 ± 3.2	22.2 ± 3.1	−0.9
Calcium salts palm	9	51.2 ± 11.3	52.5 ± 10.9	+1.3	8	23.3 ± 3.0	22.0 ± 2.8	−1.3
Calcium salts LCFA ³	8	54.4 ± 10.1	56.5 ± 8.3	+2.1	8	21.9 ± 4.4	20.3 ± 3.9	−1.4
Saturated fat	15	47.3 ± 7.5	49.9 ± 8.0	+2.6	13	23.3 ± 2.3	23.4 ± 2.1	0.1
Overall mean	96	49.6 ± 8.4	49.4 ± 9.3	−0.2	91	22.4 ± 3.4	21.3 ± 3.5	−1.1

¹Control is weighted by the number of fat treatments from each publication; Δ = treatment – control.

²MCFA = medium-chain fatty acid, C12 and C14.

³LCFA = long-chain fatty acid.

Table 5. Changes in total-tract NDF digestibility (Δ ttNDFd) and change in DMI (Δ DMI) when fat is supplemented to a lower fat control diet based on a regression model

Fat supplement type	Δ ttNDFd (%)				Δ DMI (kg/d)			
	Δ	$\Delta 3^1$	SE	P-value	Δ	$\Delta 3^1$	SE	P-value
MCFA ²	-2.65	-7.96	0.38	<0.001	-1.18	-3.54	0.15	<0.001
Oil	-0.63	-1.89	0.20	-0.01	-0.27	-0.82	0.09	0.01
C16	-0.30	-0.91	0.41	0.47	-0.06	-0.17	0.16	0.72
Animal-vegetable	-0.05	-0.16	0.33	0.87	-0.33	-0.98	0.15	0.03
Tallow	-0.11	-0.33	0.25	0.66	-0.44	-1.32	0.12	0.01
Calcium salts palm	0.54	1.61	0.34	0.12	-0.36	-1.07	0.15	0.02
Calcium salts LCFA ³	0.28	0.83	0.28	0.32	-0.43	-1.30	0.11	0.01
Saturated	0.43	1.30	0.25	0.09	0.22	0.66	0.12	0.06

¹ $\Delta 3 = 3 \times$ change (Δ) in DMI/1% increase in diet fatty acids.

²MCFA = medium-chain fatty acid, C12 and C14.

³LCFA = long-chain fatty acid.

centage units/1% FA), which has not been documented previously, though they were acknowledged as likely not having a negative effect (NRC, 2001). The magnitude of the increase was minimal, which could be why it was not detected in individual studies.

In the analysis of Δ ttNDFd/1% FA, MCFA is the only fat to significantly decrease ttNDFd (-2.9 percentage units/1%FA; Table 6, Figure 2). In this analysis, calcium salts of LCFA increased ttNDFd relative to their low-fat controls (1.1 percentage units/1%FA), which has been shown previously (Jenkins and Palmquist, 1984). The negative effect of oil in the previous model suggests

that the positive effects of calcium salts of LCFA are not due to their FA profile. Perhaps the increase is a result of their properties as a salt; this is supported by the numeric increase of ttNDFd by calcium salts of palm oil (0.4 and 0.5 percentage units/1% FA) in these analyses.

The mechanism behind the increased ttNDFd observed with calcium salts of LCFA compared with a low-fat control has yet to be fully elucidated. Calcium salts are not inert in the rumen in that they do interact with the rumen environment and undergo biohydrogenation (Van Soest and Demeyer, 1996), though

Figure 2. Forest plot of the mean change in total-tract NDF digestibility (Δ ttNDFd) from both models. ■ = Δ ttNDFd (regression model), ● = Δ ttNDFd/1% fatty acids (FA) (LSM model). MCFA = medium-chain fatty acid; LCFA = long-chain fatty acid.

Table 6. Changes in DMI (Δ DMI/1%FA) and total-tract NDF digestibility per 1% change in fatty acid (Δ ttNDFd/1%FA) when fat is supplemented to a lower-fat control diet based on an LSM model

Fat supplement type	Δ ttNDFd/1%FA (%)				Δ DMI/1%FA (kg/d)			
	Δ	$\Delta 3^1$	SE	P-value	Δ	$\Delta 3^1$	SE	P-value
MCFA ²	-2.89 ^f	-8.67	0.54	<0.001	-1.07 ^c	-3.21	0.23	<0.001
Oil	-0.42 ^e	-1.26	0.28	0.14	-0.31 ^{abc}	-0.93	0.11	0.01
C16	-0.14 ^{de}	-0.43	0.39	0.72	-0.12 ^{ab}	-0.35	0.15	0.45
Animal-vegetable	-0.09 ^{de}	-0.28	0.47	0.84	-0.19 ^{ab}	-0.57	0.18	0.31
Tallow	0.05 ^{de}	0.14	0.28	0.86	-0.32 ^{abc}	-0.96	0.12	0.01
Calcium salts palm	0.41 ^{de}	1.23	0.41	0.33	-0.40 ^{abc}	-1.19	0.16	0.02
Calcium salts LCFA ³	1.05 ^d	3.16	0.35	0.01	-0.60 ^{bc}	-1.81	0.14	<0.001
Saturated fat	0.39 ^{de}	1.17	0.32	0.23	0.23 ^a	0.68	0.13	0.09

^{a-f}Means without a common superscript differ within model ($P < 0.05$).

¹ $\Delta 3 = 3 \times$ change (Δ) in DMI/1% increase in diet fatty acids.

²MCFA = medium-chain fatty acid, C12 and C14.

³LCFA = long-chain fatty acid.

to a lesser extent than FA (Lundy et al., 2004). It is interesting to note that the average calcium content of the calcium salt diets was lower than that for the other fat-supplemented diets (mean $\pm$ SD: 0.76 ± 0.23 and $0.99 \pm 0.14\%$ DM, respectively). This suggests that the increase in ttNDFd when calcium salts are supplemented is not due to increased dietary calcium, but to another mechanism. It is possible that the UFA of calcium salts increase cholecystokinin release in the intestine (Bradford et al., 2008), thereby altering satiety and increasing digestibility (Harvatine and Allen, 2006). Though data showing that calcium salts significantly increased ttNDFd relative to control in individual studies is lacking, the combination of a small positive effect of calcium salts and a small negative effects of oils on ttNDFd may explain the greater fiber digestibility observed for calcium salts compared with other fat supplements (Jenkins and Palmquist, 1984; Doreau et al., 1993).

The models (Δ ttNDFd/1%FA, Δ ttNDFd) we tested are in agreement as to the direction of fat supplementation effects, though some differences exist in which effects reached significance between models. Overall, MCFA fats decrease ttNDFd to a degree having biological and statistical significance. Though this meta-analysis includes only 5 treatments in 2 publications, another study observed the same effects found in the meta-analysis but did not meet the requirements for inclusion (Hollmann and Beede, 2012). Those authors used 2 MCFA levels: 5% coconut oil or 2.5% coconut oil with 2.5% animal-vegetable fat. They were unable to complete the full trial, as the cows on 5% coconut oil diet were not healthy enough to continue the treatment. Data were only reported for the 2.5% treatment, in which decreases similar to those found for MCFA in the meta-analysis were observed. It can be expected that

this decrease is due to the coconut oil, as our data shows that animal-vegetable fats have no effect on ttNDFd. The significant decrease is not surprising, as Soliva et al. (2004) showed synergistic negative effects of C12 and C14 on methanogens, which could affect hydrogen levels in the rumen. Henderson (1973) showed negative effects of MCFA on other genera, such as *Ruminococcus*, which is responsible for cellulose breakdown. In contrast to these negative effects, 2 studies found no effects of MCFA fat, 1 supplemented only C12, and the other used coconut oil, on ttNDFd (Hristov et al., 2009; Faciola and Broderick, 2014), though there were significant negative effects on the quantity of protozoa in the rumen (Faciola and Broderick, 2014), which are responsible for some fiber breakdown (Hobson and Steward, 1997). Therefore, negative effects of C12 and C14 FA exist, but this is not always the case. We cannot conclude from this analysis what effect basal levels of C12 and C14 FA may have on ttNDFd even in low-fat diets.

Though oil has a statistically significant negative effect on ttNDFd, the change was only a 2 percentage unit decrease in ttNDFd at 3% FA supplementation. In a typical dairy cow ration, 3% addition of fat is equivalent to at least 0.6 kg of oil. In most cases, if this much free oil were fed negative effects on milk fat yield would likely be noted as well (He et al., 2012; Ramirez Ramirez et al., 2015; Stoffel et al., 2015), so oil additions at this level are generally avoided. It has been demonstrated that UFA can alter the microbial profile of the rumen (Ueda et al., 2003; Reveneau et al., 2012), possibly through the negative effects on the microbial membranes (Maia et al., 2007). Fats have been shown to be associated with the solid portion of the rumen mass (Legay-Carmier and Bauchart, 1989), though no evidence has shown if they directly interfere with

fiber breakdown. Ultimately, though the 2 percentage unit decrease in ttNDFd is statistically significant, it is minimal compared with the increased dietary energy density from added fat, which will be addressed later in this discussion.

The increased ttNDFd when saturated fats were supplemented may be related to their lack of effects on the ruminal environment, as they are already almost completely saturated and will have minimal negative effects on microbes (Maia et al., 2010). However, we have no explanation for why ΔttNDFd is positive rather than zero, though it is of a small magnitude. In contrast to our findings, a study not included in our data set fed 5% saturated fats to nonlactating cows and observed an average 6 percentage unit decrease in ttNDFd (Elliott et al., 1994). However, it is possible that some of this difference is due to the lower intake multiples of maintenance in dry cows (Moe et al., 1965). The other variables that could explain differences between dry cows and lactating cows differ in the remainder of the diet, including fiber sources and starch levels, which may have an effect on how fat affects fiber digestibility (Palmquist and Jenkins, 1980). However, a lack of evidence exists of an interaction between fat supplementation and forage type (Smith et al., 1993; Ruppert et al., 2003), and no interaction was determined to be significant in this analysis. The presence of a main effect in the model would have been an interaction due to the analysis of the data as a change from control.

In 90% of the treatments, fat at least partially replaced corn in the diets; therefore, the proportion of starch is decreased in the treatment diets and ttNDFd is increased approximately 0.5% for each 1 percentage unit decrease in starch (Ferraretto et al., 2013). Thus, though the data are presented as differences from controls due to addition of fat, it must be kept in mind that the treatment diets had reduced concentrations of starch and other constituents compared with control diets. On average, all diets had an increase in the sum of the NFC and FA fractions (**NFC+FA**; Table 3), which indicates that FA were substituted for other diet components in addition to NFC. This makes sense, as even if the FA were substituted for corn, some CP and NDF would be replaced. In the case of MCFA the increase in **NFC+FA** is not sufficient to explain the decreases observed in ttNDFd . The increase in **NFC+FA** could explain part of the decreased ttNDFd for oil supplemented diets. If FA depress fiber digestibility similarly to starch, as this data set suggests, then a 2 percentage unit increase in **NFC+FA** would result in a 1 percentage unit decrease in ttNDFd . This change is half of what was observed for oil supplementation. The change in **NFC+FA** is numerically less for calcium salts of LCFA

and saturated fats compared with oils and C16, which could be part of the mechanism behind the increased ΔttNDFd that are observed for calcium salts of LCFA and saturated fat. However, the lack of difference from no change for most of the fat supplements suggests that most fats have the same effect on fiber digestibility as what they replace in the diet, primarily starch.

Rumen NDF Digestibility

If fat directly suppressed NDF digestion at the site of fermentation, it is reasonable to speculate that fat could reduce NDF digestion in the rumen (**rumenNDFd**). Then, as fat is absorbed in the small intestine, the resulting digestible NDF escaping the rumen would be fermented in the large intestine. In this scenario, ttNDFd would be much less sensitive to fat effects than **rumenNDFd**. There are not enough data available for a formal statistical analysis on the changes in **rumenNDFd** by type of fat in this data set. Three studies, Doreau et al. (1993), Chelikani et al. (2004), and Brask et al. (2013), reported **rumenNDFd** to be greater than ttNDFd . Those studies were included based on the assumption that, by looking at the difference from the control to treatment, we controlled for the methodology error that was presumably present. The average change in **rumenNDFd** from fat addition ($\Delta\text{rumenNDFd}$) across fat types is a 0.4 percentage unit increase (Table 7), which contrasts with data from steers demonstrating severe negative effects of fat on rumen fiber digestibility that is made up for in the hindgut (Jenkins and Palmquist, 1984; Zinn, 1989).

The lack of a decrease in **rumenNDFd** might suggest that, although bacteria can be negatively affected by the addition of fat to the diet, especially unsaturated fats, the microbes responsible for fiber digestion are not significantly affected. This is plausible, as in vitro work has shown that bacterial metabolism has an effect on its susceptibility to high FA concentrations (Maia et al., 2007). Because this work was done in vitro, it is possible that this may not be the case in vivo, where substrate availability and passage rate are constantly changing the bacterial population. However, the changes in ttNDFd and **rumenNDFd** disagree in this data set. For oil, the mean ΔttNDFd for studies that include a **rumenNDFd** is -1.4 percentage units, which contrasts with the positive number, 3.7, found for $\Delta\text{rumenNDFd}$. Rumen digestibility is typically a more variable measurement than that for total-tract digestibility (Ueda et al., 2003; Reveneau et al., 2012; Brask et al., 2013), though this does not fully explain the discrepancies noted between $\Delta\text{rumenNDFd}$ and ΔttNDFd . The lack of a negative effect on **rumenNDFd**

Figure 3. Forest plot of the change in DMI (Δ DMI) from both models. ■ = Δ DMI (regression model), ● = Δ DMI/1% fatty acids (FA) (LSM model). MCFA = medium-chain fatty acid; LCFA = long-chain fatty acid.

supports our conclusion that a ttNDFd decrease due to oil supplementation is not biologically significant.

DMI

Changes in DMI were examined as a possible mechanism by which to explain changes in ttNDFd. One study in the data set did not report DMI and, therefore, was excluded from the analysis for DMI (Palmquist, 1991). For in-depth review of the effects of fat supplementation on intake, see Allen (2000). In the model for Δ DMI, all fats, except C16 and saturated fats, significantly decreased DMI (-0.8 to -3.5 kg/3% FA), and saturated fats tended to increase DMI (0.7 kg/3% FA). The quadratic effect of Δ FA was not

significant ($P > 0.10$) and diet FA provided a poorer fit than Δ FA in validating the analysis of the data as a linear change. Oil, MCFA, tallow, calcium salts of palm oil, and calcium salts of LCFA significantly decreased Δ DMI/1%FA (-1.1 to -0.3 kg of DMI/1% FA), and saturated fats tended to increase it (0.2 kg of DMI/1% FA; Tables 5 and 6, Figure 3).

The results from these 2 models are in agreement with the literature, which has shown decreases in DMI when fat is supplemented to the diets of lactating dairy cattle (Rabiee et al., 2012; Allen, 2000). Many of the studies used in this meta-analysis used mid-lactation cows that presumably were able to meet their energy needs for lactation without fat supplementation. Therefore, the increased dietary energy density with fat supplementa-

Table 7. Unweighted means of ruminal NDF digestibility (rumenNDFd)

Fat supplement type ¹	rumenNDFd (%; mean $\pm$ SD)			
	N	Control	Treatment	Δ
MCFA ²	2	31.1 $\pm$ 3.9	23.8 $\pm$ 11.0	-7.3
Oil	5	51.8 $\pm$ 11.7	55.5 $\pm$ 14.0	+3.7
Animal-vegetable	4	39.5 $\pm$ 10.0	38.1 $\pm$ 9.0	-1.4
Tallow	1	46.9	53.5	+6.6
Calcium salts LCFA ³	2	48.1 $\pm$ 27.2	49.6 $\pm$ 24.6	+1.5
Saturated fat	2	38.9 $\pm$ 14.2	38.0 $\pm$ 19.0	-0.9
Total	16	43.7 $\pm$ 13.2	44.1 $\pm$ 16.3	+0.4

¹No calcium salts of palm oil treatments reported rumenNDFd; Δ = treatment - control.

²MCFA = medium-chain fatty acid.

³LCFA = long-chain fatty acid.

tion could have allowed the decrease in DMI while still meeting the cows' energy requirements.

Relationship Between Δ ttNDFd and Δ DMI

A negative relationship between DMI and ttNDFd could arise from higher DMI increasing passage rate and reducing NDF digestion (Tyrrell and Moe, 1975). A positive relationship between ttNDFd and DMI could arise from increased NDF digestion causing less rumen fill and greater DMI, as shown by Oba and Allen (1999). In our data set, a significant positive relationship existed between Δ ttNDFd and Δ DMI (Figure 4). However, significance must be interpreted with caution, as the coefficient of determination was low ($R^2 = 0.06$). The inclusion of MCFA fats in the regression analysis improved the fit of the model ($R^2 = 0.20$) because of their more extreme changes in both ttNDFd and DMI compared with other fat types. As these are differences

from control, study variation has presumably been controlled for.

In contrast to the slight positive relationship between DMI and ttNDFd seen across the whole data set, we theorized a possible negative relationship for calcium salts of LCFA and palm because their means exhibited a decrease in Δ DMI and an increase in Δ ttNDFd. However, no relationship was found between Δ ttNDFd and Δ DMI (data not shown) within calcium salts. Other possible causes besides passage rate for the decrease in DMI observed with calcium salt supplementation are palatability (Grummer et al., 1990), satisfying the energy requirements at lower intakes due to increased energy density, or changes in passage rate and digestibility due to gut hormone release (Bradford et al., 2008). Saturated fats are the only fat type to have a significant relationship between Δ DMI and Δ ttNDFd, and this relationship was positive. This could suggest that cows were able to increase their DMI when ttNDFd was increased. Potential exists that Δ DMI explains some of the variability in Δ ttNDFd across fat types; however, more studies are needed to better characterize the relationship between Δ DMI and Δ ttNDFd with specific fat supplements and determine causative mechanisms.

Figure 4. Change in total-tract NDF digestibility (Δ ttNDFd) versus change in DMI (Δ DMI) for all types of fat supplement. Δ = medium-chain fatty acid (FA), $\bullet$ = all others except medium-chain FA. Regression for all (solid line): Δ ttNDFd = Δ DMI $\times$ 1.39 ($P < 0.0001$) + 0.84, $R^2 = 0.20$; Regression without medium-chain FA (dashed line): Δ ttNDFd = Δ DMI $\times$ 0.71 ($P = 0.02$) + 0.84, $R^2 = 0.06$.

TDN Changes

When fat replaces either protein or carbohydrates in a diet, it increases the dietary energy density. Therefore, an animal would be required to consume less feed to meet their energy requirements, which may be the case in this group of studies where many were mid-lactation cows. However, for high-producing dairy cattle, especially those in early lactation that are in negative energy balance, there are different constraints on intake such as fill and passage rate (Moe et al., 1965).

In this data set, the decreases in DMI had a greater negative effect on TDN intake than did any negative changes in ttNDFd. This resulted in some predicted net negative changes in TDN (Δ TDN) intakes when fat is supplemented (-2.1 to -0.1 kg/d) even though TDN concentration of the diet increased (Table 8). Therefore, when adding fat to a diet, more emphasis should be placed on potential DMI decreases than decreases in ttNDFd. Changes in DMI affect the energy derived from all nutrients, whereas changes in ttNDFd only affect NDF. Though NDF is a large portion of the diet, the NFC portion is at least as large and more digestible (NRC, 2001). The increased energy density of the diet when fat is added was not enough to maintain TDN intake when DMI decreased significantly. The small decreases in ttNDFd did not cause decreased TDN intake in any fat-supplemented diets except when MCFA or oil were supplemented.

Table 8. Predicted changes in TDN intake (Δ TDN) due to changes in DMI and total-tract NDF digestibility (ttNDFd) when 3% supplemental fatty acid (FA) is added to the diet

Fat supplement type	Predicted Δ TDN (kg/d) ¹			
	Δ FA	Δ DMI	Δ ttNDFd	Net
MCFA ²	+0.6	-2.1	-0.6	-2.1
Oil	+0.6	-0.6	-0.1	-0.1
C16	+0.6	-0.2	0.0	+0.4
Animal -vegetable	+0.6	-0.4	0.0	+0.2
Tallow	+0.6	-0.6	0.0	0.0
Calcium salts palm	+0.6	-0.8	+0.1	-0.1
Calcium salts LCFA ³	+0.6	-1.2	+0.2	-0.4
Saturated fat	+0.6	+0.5	+0.1	+1.2

¹Means from Δ ttNDFd/1% FA and Δ DMI/1%FA were utilized. Δ FA is the increase in TDN intake due to the increased energy density of the diet with 3% fat supplementation, Δ DMI is the change in TDN intake with a fat supplemented diet with and without a change in DMI due to fat supplementation, Δ ttNDFd is the change in TDN intake with a fat supplemented diet with and without a change in ttNDFd due to fat supplementation.

²MCFA = medium-chain fatty acid.

³LCFA = long-chain fatty acid.

The digestibility of fat supplements was not altered from 75% for the purpose of this simulation. There is a range of fat digestibility across fat supplement types, with calcium salts generally having higher digestibilities than hydrogenated fats due to the difference in C18:0 content (NRC, 2001; Boerman et al., 2015). Therefore, the differences in Δ TDN intake may not be quite as large as they appear, particularly between calcium salts, negative Δ TDN, and hydrogenated fats, positive Δ TDN (Table 8).

CONCLUSIONS

Dietary SFA with 12 or 14 carbons reduced ttNDFd and DMI. Oils appear to have had only a small negative effects on ttNDFd, but these were relatively unimportant at levels of oils typically fed, and ttNDFd changes were small compared with changes in DMI and energy density increases due to substituting fat for carbohydrate. Inclusion of calcium salts of LCFA or saturated fats may have actually increased ttNDFd. No other 16- or 18-carbon fat significantly affected ttNDFd, and these fats also do not appear to have had significant effects on rumen NDF digestibility at levels fed in these studies. The increased ttNDFd due to the supplementation of calcium salts was not related to concurrent decreases in DMI, indicating another mechanism besides changes in DMI is responsible for the ttNDFd increase.

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